RAPID GROWTH RATES IN INFLORESCENCES OF Xanthorrhoea australis R. Br.

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ABSTRACT: Developing inflorescences of Xanthorrhoea australis growing at Mt. Slide, Victoria, were measured at weekly intervals until growth in length had ceased. A maximum growth rate of 49 cm for 7 days (an average of 7 cm per day) was recorded. Maximum diameter at the base was 5 cm while the maximum length of inflorescence of 300 cm was attained over about 75 days growth—an average of 4 cm per day. Weekly rhythmic fluctuations in growth rates were observed and relative growth rates in length were maximal in weeks one and four of the measurements. No clear relation between rainfall and growth was found and doubts are cast on the presumed longevity of plants of the genus Xanthorrhoea.

INTRODUCTION

From the time of botanists such as Saehs (1875), Pfeffer (1903) and Jost (1907) to present times, much rescarch has been donc on the measurement and evaluation of growth rates of roots, stems and leaves. Mcasurement of the growth rates of inflorcseences, however, secms to have been largely neglected, even though elongation rates of some floral parts such as anther filaments have been carefully documented (Askenasy 1879). This report gives data collected from plants of the arborescent monocotyledon Xanthorrhoea australis R. Br., whose inflorescences reach a height of 3 metres (approximately 10 feet) within 11 weeks, although produced by a vegetative stem that protrudes only 1.5 m above soil level. These rapid growth rates occur in a dry sclerophyll forest where annual rainfall fluctuates between 84 and 145 em (33-57 inches). The only other published report of inflorescence growth in Xanthorrhoea comes from Clcland (1913) who described measurements he made on a single inflorescence of X. hastilis R. Br.

MATERIALS AND METHODS

Between September and December 1968, approximately weekly measurements of infloreseence lengths of 20 plants of *Xanthorrhoea australis* were made including those shown in Pl. 18, fig. 1. These 20 were the only plants that flowered in the normal flowering season of 1968 in a large stand of several thousand plants located on the slopes of Mt. Slide, Victoria (37°32'S, 145°22'E). The normal flowering season extends between September and December, but the passage of a fire through a stand usually stimulates the plants to flower. Specht and Rayson (1957a), working in South Australia, observed flowering of X. australis only after plants had been burnt. In field work done in 1972, Gill and Ingwersen (pers. comm.) worked on stands of X. australis in south-eastern Australia. They found that experimentally burned plants produced inflorescences 80 days earlier than control plants in which infloresecnces first appeared after 235 days. No firc had passed through the study area at Mt. Slide within the last two years as evidenced by the long, dead persistent 'skirts' of leaves visible around many of the plants' stcms.

RESULTS

Each inflorescence produced by X. australis has a basal, cylindrical, faintly-ribbed, infertile, green scape, whose length ranges from 40-90 em, and whose basal diameter is between 3-5 cm. The scape subtends a long, slightly-tapering spike with myriads of sessile flowers subtended by brown, scaly braets that are prominent before anthesis, and give the developing spike a brown colour. Pl. 18, fig. 2, 3 show developing inflorescences protruding from above the mass of narrow, linear leaves that are produced by the stem.

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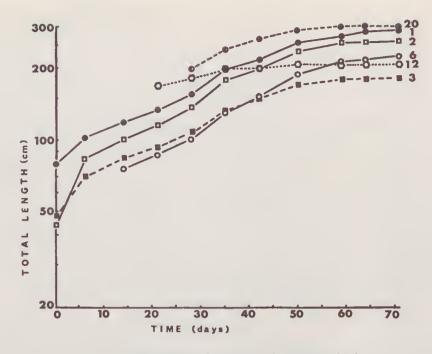
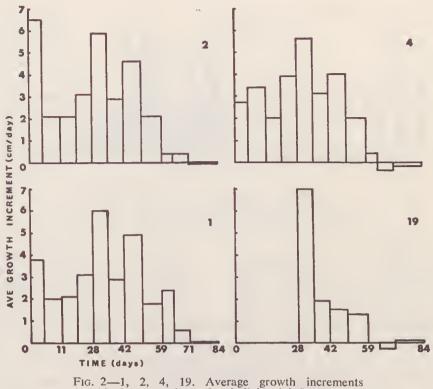


FIG. 1—Logarithmic plot of total length of six individual inflorescences (cm) versus time (days)

The plant's axis is sympodial, i.e. the inflorescence is terminal. The vegctative shoot apex is massive in size, of the order of 1.3 µm in diameter, similar to that described for X. mediathe largest vegctative shoot apex yet recorded in the monocotyledons (Staff 1968). The terminal shoot apex of X. australis is normally converted into an inflorescence during the months of August to December, and the percentage of flowering is not high in a particular stand unless it has been burnt. As the numerous young leaves of the plant obseure young inflorescences from view, lengths cannot be measured until the inflorescences become visible. This resulted in initial measurements of inflorescences no shorter than 50 cm, and sometimes as long as 190 cm.

Fig. 1 shows the growth in total length of six inflorescences over a time of 178 days, while Fig. 2 shows the relation between average growth increment in length (cm) per day, versus time for four different inflorescences. Maximum growth rates occurred between days 28 and 35, and the highest growth rate observed was 49.0 cm per week, an avcrage of 7.0 cm per day (Fig. 2-19). In many of the plants measured, three peaks of high growth rates occurred between days 1-6 (weck 1), 28-35 (week 5) and 42-50 (week 7), but a graph of average growth rates for all plants (Fig. 3) had only two pcaksone in week 1 and the second in week 5. Variability in these results may be due to several factors such as variations in habitat within the communities, in genotype, and in age or size of plants, but it was thought that significant variations could be duc especially to variations in physiologieal maturity of the plants measured. As an indication of the last criterion mentioned, an example can be drawn from the data presented in Fig. 2. Maximum anthesis of these inflorescences occurred during weeks 9, 9, 7, 6 for plants numbered 1, 2, 4, and 19 respectively. In an attempt to remove some of the irregularities caused by this variation in physiological age, and also in sizes of inflorescences, the length measurements were all converted to percentages of the maximum length attained by each inflorescence. The first 100% reading obtained chronologically for an inflorescence was taken as the last reading on the extreme right hand side of the new graph. The net effect was to standardize all the graphs for maximum size attained to 100%, as well as to transpose laterally graphs of plants that were out of phase physiologically with other inflorescences—e.g. the curve for plant no. 12 was moved back two weeks by this procedure (i.e. to the right with relation to other inflorescences). Fig. 4 makes a comparison between the average total length measurements plotted on the actual days that readings were collected and the adjusted plot. It can be seen that the latter graph provides



(cmi/day) versus time of 4 individual inflorescences.

less variation in the standard errors of the mean, and probably gives a more meaningful indication of the average lengths of plants at similar growth phases. The curve thus obtained is biphasic, with the first sigmoid curve extending over days 0-21, followed by a second, protracted growth curve.

To see if there were any closely defined relationship between growth rates and rainfall, a plot of average growth rates (cm/day) was made on the same graph as rainfall, which was recorded for 11 weeks prior to and during the time span of the measurements (Fig. 3). No obvious link was seen and, in fact, during weeks with high growth rates (1 and 5), rainfall was low.

DISCUSSION

Kraus (1895) reported rapid growth rates of 977 cm in 7 days (139.6 cm/day) for a shoot of a bamboo, Bambusa arundinacea. He also reported that a shoot of Bambusa gigantea grew 7.85 m in length in 31 days, an average of $25 \cdot 3 \text{ cm/day}$. Pfeffer (1903) recorded the production of 12 m of stems in a summer by species of Humulus and Cucurbita. The growth rates reported in this paper, when calculated on the basis of growth coefficients, or % increase of biomass, may not be as impressive as the growth rates of staminal filaments of Triticum and Secale (from a length of 4 mm to 7 mm in 2 minutes, Askenasy 1879). Nevertheless, the production of a massive stem in a relatively short time is always spectacular.

In Xanthorrhoea australis, the inflorescence, a determinate structure, attains a maximum length of 300 cm, and maximum diameter of 5 cm in a time span of about 75 days—an average of 4 cm/day with a maximum growth of 7 cm/ day. The measurements made by Cleland (1913) on a single inflorescence of X. hastilis in Sydney showed a maximum elongation rate of 10.2 cm, which was maintained for three days, but the average growth rate over the period of observation, 60 days, was 3.0 cm/day. Gill and Ingwersen (1974) examined inflorescence growth in X. australis and found maximum elongation rates of 5 cm/day. This is a particularly interesting phenomenon, especially when one considers that such growth rates occur in a climate that is relatively cooler and drier than the tropical climates where such impressive growth rates of bamboos have been observed. Hartley (1969) recorded lengths of oil palm inflorescences of 40 cm developing in 3-4 months from small size, and this does not represent as rapid a growth in length as the Xanthorrhoea inflorescences.

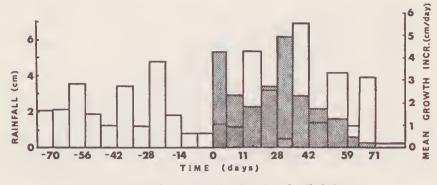


FIG. 3—Mean increment in length of all inflorescences/day versus time (weeks) (shaded), and rainfall (cm) at Kinglake Post Office from July 1 to December 9, 1968 (unshaded).

In Australia, the growth rate of the vegetative stem of the grass tree has traditionally been thought to be very slow, Lewis (1955) attempted to estimate the ages and growth rates of some specimens of X. australis. He suggested, on the basis of production of $2\frac{1}{2}$ leaves per annum of some seedlings, that plants may be over 6,000 years old by the time that the stem reaches maturity at soil level (the stems of seedlings usually develop underground). Such an extrapolation is extremely misleading, as annual leaf production by plants rapidly increases after the first few years of establishment growth. Gill and Ingwersen (1974) working with stands of Xanthorrhoea in forests of Pinus and Eucalyptus, and in grasslands, were able to eorrelate burn sears on the plants with known dates of fires. This allowed them to establish for these plants a maximum elongation rate of stems of 3.1 em/ year for a period of 21 years. At this growth rate, a height of 300 cm (nearly 10 feet) would take 97 years to be produced. It is thus likely that estimates of great age of such plants are grossly in excess of actual age, which are probably of the order of 100 to 250 years.

From the data presented here, several significant points become apparent. First, by examining Figs. 1 and 2, it is elear that growth rates of individuals fluctuate considerably from week to week. In many plants, a week of high growth rate is often followed by a week of lower growth rate. It seems reasonable to interpret this as an example of rhythmic growth, the effect of which is not necessarily shown in the averages subsequently presented (Figs. 3, 4). Hallé and Martin (1968) have studied endogenous rhythmic growth phenomena of *Hevea brasiliensis* in the tropics. They found a repetitive cycle of 42 days, and suggested that one of the major factors responsible was competition between the apical meristem and the leaves for water. They also noted rhythmic growth in species of the woody monocotyledon *Dracaena*, and reviewed some of the relevant literature on rhythmie growth in tropical and temperate regions. Although he did not remark on it, rhythmic growth with a periodicity of 2 days can even be seen in data presented by Sachs (1875) on the growth of the flowering stem of *Fritillaria imperialis*. Cleland (1913) noted a diurnal variation of elongation in an inflorescence of *X*. *hastilis*, where most of the elongation occurred in the night.

Pl. 18, fig. 4 illustrates an unusual case of one inflorescence of X. australis, found at Anglesea, Vietoria, whose growth resulted in a sinuous spike and in which the undulations eould have been governed by rhythmic growth factors. However, as no data were collected on the growth of this inflorescence, it is impossible to know what were the actual causal factors that controlled this strange growth form.

Second, when an adjustment for varying growth phases of the plants, and for differences in final inflorescence height is made, a plot of average length versus time still shows a biphasic growth curve, with maximum growth rates occurring in weeks 1 and 4. Obviously, the first growth maximum is only partly recorded because of the difficulty in finding infloreseences in the field at very early stages of development, and the second one eorresponds to the spurt of growth that precedes anthesis. As the gradient of the plot of growth in total length on a logarithmic scale versus time gives an indication of Relative Growth Rate (Evans 1972)-in this instance, growth rate relative to intial length-it is apparent from the adjusted plot in Fig. 4 that the highest relative growth rates (in length) occurred in weeks 1 and

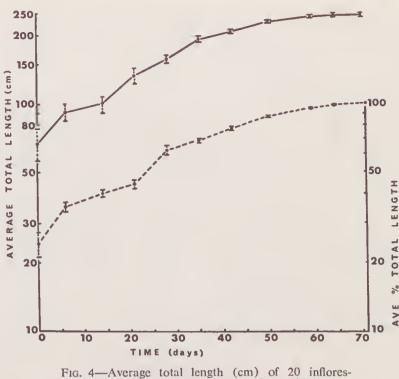


FIG. 4—Average total length (cm) of 20 inhorescences versus time (upper curve with solid line) logarithmic scale on ordinate. Average length (% total final length) of 20 inflorescences adjusted for similar physiological maturity (lower curve dashed line)—logarithmic scale on ordinate.

4. The steepest gradient of the graph in this figure occurred in week 1, and thus the maximum relative growth rate in length occurred in week 1, although the highest absolute growth increments per day occurred later, in week 4. In other words, in week 1, an increase from 24 to 35 cm represents an increase of 46% over the initial length, but in week 4, an increase from 44 to 62 cm represents an increase of 41% in length.

Although Specht and Rayson (1957b) showed that X. australis plants growing in sandy soil had a great capacity to intercept rain and to concentrate water in the soil immediately underneath the plants, no clear relation between rainfall and inflorescence growth could be seen in the present work. It is apparent that data on solar radiation and temperature should have been obtained to gain a better view of the effect of environment on inflorescence growth. Fitzpatrick and Nix (1970) in discussing the climatic factor in Australian grassland ecology, stress the need for quantifying climatic factors such as light, temperature and precipitation and do so in terms of a 'Thermal Index', a 'Light Index' and a 'Moisture Index'. For the oil palm, from work by Hartley (1967) and Brockmans (1957), the production of large, fertile inflorescences is greatly dependent on water availability even up to 2 years preceding the time of inflorescence maturation. This is understandable, as the inflorescence primordium may still be present in the leaf axil during the time of water deficiency. A parallel situation for X. australis inflorescence primordia does not exist, as they arc not long-lived and further studies would be necessary in order to clarify the relationship between inflorescence growth and water availability.

Finally, the collection of data on the growth of inflorescences is a scantily researched field of investigation. Because of the almost cylindrical and unbranched form of the inflorescence of *Xanthorrhoea australis*, useful data can be obtained from these plants. The difficulties of collection of the data include low percentage flowering in unburnt stands and inaccessibility of the plants for regular measurement.

ACKNOWLEDGMENTS

I thank Mr. R. H. Norweb III, who acted as a research assistant while a visiting student from Beloit College, Beloit, Wisconsin, U.S.A. The manuscript was finalized while the author was a Charles Bullard Research Fellow at Harvard Forest, Petersham, Massachusetts, U.S.A., on study leave from La Trobe University. The rainfall data were provided by Mrs. M. McMinn, Kinglake Post Office.

REFERENCES

- ASKENASY, E., 1879. Ueber das Aufblühen der Gräser. Verhandl. d. Naturh.-Med. Vereins zu Heidelberg N.F. 2: 261-273.
- BROEKMANS, A. F. M., 1957. Growth, flowering and yield of the oil palm in Nigeria. J. W. Afr. Inst. Oil Palm Res. 2: 187-220.
- CLELAND, J. B., 1913. Note on the growth of the flowering stem of Xanthorrhoea hastilis R. Br. J. & Proc. R. Soc. N.S.W. 47: 72-74.
- Evans, G. C., 1972. The quantitative analysis of plant growth. In *Studies in Ecology*, Vol. 1. Blackwell Sei. Pub., Oxford, 734 pp.
- FITZPATRICK, E. A. & NIX, H. A., 1970. The climatic factor in Australian grassland ecology. In Australian Grasslands, pp. 3-26. Ed. R. M. Moore. A.N.U. Press, Canberra. 455 pp.
- GILL, A. M. & INGWERSEN, F., 1974. (Pers. comm.). Division of Plant Industry, CSIRO, Canberra, A.C.T.
- HALLÉ, F. & MARTIN, R., 1968. Etude de la croissance rhythmique chez l'Hevea brasiliensis Müell.-Arg. Adansonia, sér. 2, 8: 475-503.

- HARTLEY, C. W. S., 1967. The oil palm (Elaeis) guineensis). Longmans, London.
 - , 1969. Some environmental factors affecting flowering and fruiting in the oil palm. Pp. 269-286. In *Physiology of tree crops*. Eds. L. C. Luekwill and C. V. Cutting. Academic Press, N.Y.
- Jost, L., 1907. Lectures on plant physiology. Translated by R. J. Harvey Gibson. Clarendon Press, Oxford.
- KRAUS, G., 1895. Physiologisches aus den Tropen. Ann. du Jard. Bot. Buitenzorg 12: 196-216.
- LEWIS, C. F., 1955. Observations on the age of the Australian grass tree, Xanthorrhoea australis. Vic. Nat. 72: 124-125.
- PFEFFER, W., 1903. The Physiology of Plants Vol. II. Trans. & Ed. A. J. Ewart. Clarendon Press, Oxford.
- SACHS, J., 1875. Text-book of Botany—morphological and physiological. Trans. A. W. Bennett and W. T. Thiselton Dyer. Clarendon Press, Oxford.
- SPECHT, R. L. & RAYSON, P., 1957a. Dark Island heath (Ninety mile plain, South Australia).
 I. Definition of the ecosystem. Aust. J. Bot. 5: 52-85.
- (Ninety mile plain, South Australia). IV. Soil moisture patterns produced by rainfall interception and stem flow. *Ibid.* 5: 137-150.
- STAFF, I. A., 1968. A study of the apex and growth patterns in the shoot of Xanthorrhoea media R. Br. Phytomorphology 18: 153-166.

DESCRIPTION OF PLATE 18

FIG. 1—Part of the study area at Mt. Slide, Vietoria, with specimens of Xanthorrhoea australis in flower. (Total length of inflorescence at left is 250 cm.)

FIGS. 2, 3—Two stages in the development of an inflorescence. (Total lengths are 83 and 100 cm respectively.)

FIG. 4—Unusually curved inflorescence observed at Anglesea, Victoria. (Total height is 170 cm.)